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COMPARATIVE MORPHOLOGY OF THE FOLIAR SCLEREIDS
IN THE GENUS *MOURIRIA* AUBL.

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With eleven plates

INTRODUCTION

A RECENT intensive study of the foliar sclereids of *Trochodendron aralioides* revealed the remarkable fluctuation in the form and structure of such cells which occur within a single species (10). Because of this polymorphism, one might question the diagnostic value of foliar sclereids in the distinction of species, genera, and tribes within the angiosperms, despite the extensive literature which has accumulated on this subject (cf. the resumé in Solereder, 20). Upon careful examination, much of the early systematic work on foliar sclereids seems inadequate for two reasons. First of all, in many cases the morphological observations are not correlated with specific herbarium collections. Secondly, very little attention is paid to the possibility of variation in sclereid-type between different leaves of one individual and between leaves of different individuals of the same species. As a result, it is hazardous or indeed impossible in many instances to generalize with respect to the major trends in morphological specialization of foliar sclereids within systematic units. Further evidence of the present uncertainty of our knowledge is provided by the investigations of Bailey and Nast (5) on the variable trends of specialization in the foliar sclerenchyma of the species and genera in the Winteraceae.

It is evident, therefore, that intensive and rigorously documented studies on the foliar sclereids of a wide series of genera are highly desirable. In the present article the results of a comparative study of the foliar sclereids of *Mouriria* Aubl. (Melastomataceae) are presented. This genus, according to van Tieghem (21), exhibits a wide range of sclereid-types, each of which is illustrated by a series of species. Moreover, the consistent presence of foliar sclereids in *Mouriria* as well as in the presumably closely related genus *Memecylon* L. was utilized by van Tieghem as the

basis for segregating these genera in the subtribe "Mouririées" under the family "Mélastomacées." Unfortunately, however, van Tieghem included neither the author-names of the species of *Mouriria* studied nor citations to specific herbarium specimens. Consequently in the present study a complete re-examination of the foliar sclereids of *Mouriria* has been made, utilizing an extensive series of herbarium collections.

In Cogniaux's (7) monographic treatment of *Mouriria*, 40 species and one "species non satis nota" are recognized. Since the publication of his work many new entities have been described, so that the genus now contains approximately 80 species. The present survey is based upon the examination of 69 species and includes material representing all but 6 of the entities included by Cogniaux as well as all the species discussed by Hoehne (12) and Ducke (8). While it is recognized that some of the entities used may subsequently prove to have been incorrectly determined, the morphological descriptions are based on cited specimens and are thus subject to verification. Furthermore, in the majority of species examined, two or more separate collections were available, thereby permitting some study at least of morphological variations. In the case of 17 species, leaves from the type collection were investigated. Although the importance of type material should not be over-rated in a study of this sort, morphological data on such specimens will need to be considered in any future revision of the genus.

Grateful acknowledgement is made to my wife, Helen Vincent Foster, for her drawings of the sclereids illustrated in *Plate XI*. The writer also thanks Professor I. W. Bailey and Dr. A. C. Smith for many helpful comments during the progress of the investigation.

MATERIALS

The herbarium leaf-specimens forming the material for this investigation were secured through the generous coöperation of the following individuals: Dr. A. C. Smith, of the Arnold Arboretum (A); Dr. Paul C. Standley, of the Chicago Natural History Museum (Ch); Dr. J. M. Greenman, of the Missouri Botanical Garden (M); Dr. H. A. Gleason, of the New York Botanical Garden (NY); Dr. E. P. Killip, of the U.S. National Herbarium (US); Dr. Lyman B. Smith, of the Gray Herbarium (GH); Dr. H. L. Mason, of the University of California (UC); Dr. C. L. Wilson, of Dartmouth College (Dart); and Dr. J. T. Roig, of the Estación Experimental, Santiago de las Vegas, Cuba (Cu). Through the kindness of Dr. F. C. Hoehne of the Instituto de Botanica at São Paulo and Dr. J. G. Kuhlmann of the Jardim Botânico at Rio de Janeiro, a separate collection of leaf-specimens of 30 species of *Mouriria* has also been investigated. This material is derived from specimens deposited in the herbarium of the Jardim Botânico (HJBR). The writer is also indebted to the authorities of the Instituto Agrônômico do Norte, Belem, Pará, Brazil, for dried and preserved leaves of *M. crassifolia* Sagot. This valuable material

was collected "in virgin forest 8 km. from Manaus" by J. P. Murça and was determined by Dr. A. Ducke.

For convenience in reference, the species used in the present study have been arranged below in alphabetical order. At the end of this list are appended a number of undetermined specimens. In all cases, the symbol in parentheses following the citation of each specimen designates one of the herbaria listed above. An asterisk preceding a species name indicates that material from the type collection has been studied.

- M. abnormis* Naud. FRENCH GUIANA: Mélinon in 1861 (Ch).
 **M. acuta* Griseb. CUBA: Wright 2469 (M, TYPE COLL.); Jack 7955 (Ch); Britton, Britton & Cowell 9730 (NY, US); Jack 5741 (A); Ekman 16384 (US).
M. acutiflora Naud. BRAZIL: Ule 7677 (UC); Kuhlman 4546 (HJBR); Ducke 18497 (HJBR); HJBR, Rio Madeira, Amazonas; Krukoff 26653 (HJBR); Ducke 18500 (HJBR). BRITISH GUIANA: A. C. Smith 2573 (A); A. S. Pinkus 195 (US).
 **M. acutiflora* var. *oligantha* Gleason. SURINAM: B. W. 6286 (US, TYPE COLL.).
 **M. angustifolia* Spruce. BRAZIL: Spruce 2987 (GH, TYPE COLL.).
M. anomala Pulle. BRAZIL: Ducke 14373 (HJBR, US); Ducke 105 (Ch); Ducke 25515 (HJBR).
M. Apiranga Spruce. BRAZIL: da Costa 124 (Ch); Ducke 18495 (HJBR); Ducke 35736 (HJBR). PERU: Ule 9678 (US).
 **M. arborea* Gardn. BRAZIL: Gardner 5704 (GH, NY, TYPE COLL.).
M. brachyanthera Ducke. BRAZIL: Mexia 5964 (UC); Ducke 35737 (HJBR); Ducke 10870 (HJBR).
 **M. brachypoda* Urban & Ekman. HAITI: Ekman 6064 (US, TYPE COLL.). SANTO DOMINGO: Ekman H14694 (NY); Ekman H6257 (A).
M. brevipes Benth. SURINAM: B. W. 1506 (Ch); Utrecht Herb. 1506 (US); Plantae Surinamenses 1506 (NY). BRAZIL: Ducke 27605 (HJBR).
M. brunneicalyx Standley. PANAMA: Seibert 609 (A).
M. buxifolia Urban. SANTO DOMINGO: Ekman 11295 (A).
M. caudiflora DC. BRAZIL: Ducke 25517 (HJBR, US). PERU: Klug 1374 (Ch).
M. cearensis Huber. BRAZIL: Ducke 14378 (HJBR).
M. Chamissoana Cogn. BRAZIL: Glaziou 44803 (Ch); Hoehne 29921 (NY); Sellow 473 (US); Porto 10759 (HJBR); Ducke 6561 (HJBR).
M. Chamissoana var. *padlistana* Hoehne. BRAZIL: Hoehne 29921 (Ch); Hoehne 27704 (A).
M. ciliata Gleason. BRAZIL: Krukoff 5478 (UC).
M. collocarpa Ducke. BRAZIL: Ducke 299 (US); Ducke 25516 (HJBR); Ducke 35740 (HJBR).
M. crassifolia Sagot. FRENCH GUIANA: Mélinon in 1862 (Ch); Mélinon in 1864 (A). SURINAM: Utrecht Herb. 3358 (US). BRAZIL: Ducke 27624 (HJBR).
M. cyphocarpa Standley. BRITISH HONDURAS: Schipp 70 (UC); Gentle 2126 (NY); Lundell 6945 (US). MEXICO: Williams 9398 (A).
M. densifoliata Ducke. BRAZIL: Ducke 801 (M); Ducke 50951 (HJBR).
M. domingensis Spach. SANTO DOMINGO: Ricksecker 477 (UC). HAITI: Ekman H4209 (NY, US); Ekman H5121 (A).
M. Doriana Saldanha. BRAZIL: Brade 11203 (GH); Saldanha 14418 (HJBR).
M. diometosa Cogn. BRAZIL: Ducke 22518 (HJBR, US).
M. elliptica Mart. BRAZIL: Capanema 19620 (HJBR).
 **M. emarginata* Griseb. CUBA: Wright 2467 (M, TYPE COLL.); Ekman 7443 (NY); Ekman 9280 (US).
M. eugeniaefolia Spruce. BRAZIL: Spruce, Dec.-Mar. 1850 (GH).
M. exilis Gleason. GUATEMALA: Wilson 497 (Ch). BRITISH HONDURAS: Schipp 70 (NY); Gentle 2927 (A).
M. floribunda Markgraf. PERU: Mexia 6187 (UC).

- M. Gardneri* Triana. BRAZIL: *Gardner* 2863 (GH); *Gardner* 4154 (NY).
- **M. Gleasoniana* Standley. MEXICO: *Matuda* 3093 (Ch, TYPE COLL.). GUATEMALA: *Steyermark* 39525 (Ch).
- M. grandiflora* DC. PERU: *Williams* 8128 (Ch). BRAZIL: *Ducke* 18504 (HJBR).
- M. guianensis* Aubl. BRAZIL: *Drouet* 2356 (UC); *Krukoff* 11926 (NY); *Krukoff* 6613 (A); *Huber* 10873 (HJBR); HJBR, Amazonas. FRENCH GUIANA: *Broadway* 434 (US). VENEZUELA: *Williams* 11600 (US).
- M. Helleri* Britton. PUERTO RICO: *Heller* 1372 (Ch, NY).
- **M. hottensis* Urban & Ekman. HAITI: *Ekman* 10399 (A, US, TYPE COLL.).
- M. Huberi* Cogn. BRAZIL: *Mexia* 5980 (UC); HJBR, Pará.
- **M. lanceolata* Griseb. CUBA: *Wright* 1235 (M, TYPE COLL.); *Ekman* 15810 (US).
- M. Lisboa* Huber. BRAZIL: *Lisboa* 11462 (HJBR).
- **M. marstralis* Urban. CUBA: *Ekman* 9350 (NY, US, TYPE COLL.).
- **M. Marshallii* Burt Davy & Sandwith. TRINIDAD: *Russell* 1265-9 (NY).
- **M. micradenia* Ducke. BRAZIL: *Ducke* 25520 (HJBR, US, TYPE COLL.).
- M. monantha* Urban. CUBA: *Ekman* 4415 (US).
- M. Muelleri* Cogn. MEXICO: *Matuda* 3339 (M); *Matuda* 3093 (A); *Reko* 3817 (US).
- M. myrtifolia* Spruce. BRAZIL: *Krukoff* 1371 (A, UC); *Krukoff* 1407 (A); *Ducke* 14379 (HJBR).
- M. myrtilloides* Poir. CUBA: *Herb. Richard* (Ch). JAMAICA: *Britton* 3098 (NY); *Harris & Britton* 10629 (US).
- M. nervosa* Pilger. BRAZIL: *Ducke* 205 (A); *Ducke* 14388 (HJBR).
- M. oligantha* Pilger. PERU: *Williams* 3904 (Ch).
- M. parvifolia* Benth. MEXICO: *LeSueur* 647 (GH). BRITISH HONDURAS: *Gentle* 44 (UC); *Schipp* 124 (UC); *Lundell* 483 (UC); *Gentle* 3712 (NY); *Bartlett* 13132 (US). PANAMA: *Pittier* 5711 (US); *C. L. Wilson* acc. No. 101 (Dart). ECUADOR: *Rimbach* 92 (NY, US). BOLIVIA: *Steinbach* 7582 (GH).
- M. Petroniana* Cogn. & Sald. BRAZIL: *Glaziov* 13860 (Ch); *Almeida* 48224 (HJBR).
- M. Plasschaerti* Pulle. BRAZIL: *Ducke* 17234 (US); *Ducke* 14383 (HJBR).
- M. princeps* Naud. BRAZIL: *Krukoff* 5459 (UC); *Krukoff* 8412 (A); *Krukoff* 5986 (A); HJBR No. 27622. PERU: *Killip & Smith* 29761 (Ch).
- M. pseudo-geminata* Pittier. VENEZUELA: *Williams* 10182 (Ch).
- M. Pusa* Gardn. BRAZIL: *Glaziov* 19348 (Ch); *Gardner* 2596 (NY, US); *Brade & Barreto* 45553 (HJBR); *Ducke* 14392 (HJBR).
- M. rhizophoraefolia* Triana. TOBAGO: *Broadway* 4622 (Ch, US); *Broadway* 3976 (GH).
- **M. rostrata* Urban. CUBA: *Ekman* 14069 (GH, US, TYPE COLL.); *Collector?* (NY).
- M. Sagotiana* Triana. SURINAM: *B. W.* 5475 (Ch). PERU: *Kiug* 1501 (US). BRAZIL: *Ducke* 10866 (HJBR); HJBR, no locality given.
- **M. samanensis* Urban. SANTO DOMINGO: *Abbott* 2233 (M, TYPE COLL.); *Ekman* 15180 (A); *Ekman* 14895 (A).
- M. Sideroxylon* Sagot. PERU: *Killip & Smith* 26845 (Ch, US).
- M. spathulata* Griseb. CUBA: *Shafer* 3254 (US); *Wright* 1234 (GH).
- M.* "aff. *spathulata* Griseb." PUERTO RICO: *Sintensis* 6195 (A); *Sintensis* 6095 (US).
- **M. Steyermarkii* Standley. GUATEMALA: *Steyermark* 39416 (Ch, TYPE COLL.).
- **M. subumbellata* Triana. BRAZIL: *Spruce* 2004 (GH, TYPE COLL.).
- **M. trunciflora* Ducke. BRAZIL: *Ducke* 16937 (US, TYPE COLL.); *Capucho* 456 (Ch); *Ducke* 10839 (HJBR).
- M. Ulei* Pilger. BRAZIL: *Ducke* 205 (Ch); *Ule* 7677 (US); HJBR, Pará.
- **M. Valenzuelana* A. Rich. CUBA: *Wright* 2468 (M, TYPE COLL.); *Ekman* 13845 (A, Ch, NY, US).
- M. vernicosa* Naud. FRENCH GUIANA: *Mélinon* 189 (Ch); *Martin* s.n. (GH). SURINAM: HJBR, no locality given.
- M. Weddellii* Naud. BRAZIL: *Gardner* 2595 (US); *Lützelberg* 5998 (HJBR).
- M. sp.* BRAZIL: *Krukoff* 6565 (A).
- M. sp.* BRAZIL: *Krukoff* 6706 (A).

- M. sp.* BRAZIL: *Ducke 44* (A).
M. sp. BRAZIL: *Ducke 173* (A).
M. sp. BRAZIL: *Ducke 299* (A).
M. sp. CUBA: *Acuña 12602* (Cu).
M. sp. CUBA: *Acuña 12603* (Cu).
M. sp. CUBA: *Acuña 12604* (Cu).
M. sp. CUBA: *Acuña 7724* (Cu).
M. sp. CUBA: *Bucher 191* (Cu).
M. sp. CUBA: *Roig 61* (NY).

TECHNIQUE

Most of the data presented in this paper are based upon the study of cleared leaves. The technique consists in removing the pigments by treatment with 5% NaOH in an electric oven followed by dehydration in alcohol and clearing in xylene. The preparations were mounted directly in balsam without staining. In the case of large-leaved species, comparable portions of the lamina including the marginal and midrib areas were used. In many of the small-leaved species, the entire cleared lamina could be mounted beneath the cover-glass.

The study of cleared leaves was supplemented, when necessary, by hand-sections and by macerations. In most instances, the sclereids could be readily isolated from the surrounding leaf-tissue by teasing apart small portions of the thoroughly cleared laminae in a drop of water on a slide. The use of acid-alcohol followed by treatment with very dilute ammonium oxalate was particularly helpful where the sclereids are firmly adherent to the mesophyll and epidermal cells. In all cases the isolated sclereids were mounted directly from water into glycerine jelly.

DISTRIBUTION OF SCLEREIDS IN THE LAMINA

One of the most interesting and unexpected results of this study was the discovery that, throughout the species examined, the sclereids tend to be restricted to the ultimate ends of the veinlets (*figs. 1-15, 31-34*). This prevaillingly *terminal position* of the foliar sclereids in *Mouriria* contrasts strikingly with the more usual *diffuse* distribution of such cells in the leaves of other dicotyledons (5, 9, 10, 11, 20). Despite the relatively large number of species studied by van Tieghem (21), he overlooked this definitive topographical feature of *Mouriria*, as did Palézieux (15), probably because both investigators made their observations largely on leaf-sections. A more detailed discussion of the morphological and ontogenetic implications of the terminal position of the sclereids will be deferred until the various sclereid-types in *Mouriria* have been described.

In addition to terminal sclereids, a number of species examined develop small unbranched sclereids in the tissues of the midrib and the short petiole. These sclereids occur either as solitary cells or are clustered, and appear to fluctuate in abundance even within the same species. Somewhat similar cells, with numerous pits, were also found lying free in the mesophyll

of the leaves of *M. angustifolia*, *M. cauliflora*, *M. cyphocarpa*, *M. exilis*, *M. oligantha*, and *M. trunciflora* (figs. 10, 21). In these species, the diffuse sclereids tend to be most numerous in the vicinity of the midrib and the larger veins but their distribution and abundance fluctuate considerably. In *M. oligantha*, for example, small diffuse sclereids were encountered even in the extreme marginal region of the lamina scattered among the large, irregularly branched terminal sclereids.

SCLEREID TYPES

In agreement with the observations of van Tieghem (21), the present survey reveals an extraordinary range in the form of the foliar sclereids in *Mouriria*. The majority of the species develop more or less conspicuously branched sclereids which vary widely in respect to the form of the cell-body and the position and extent of the system of branches. In marked contrast, a relatively few species exhibit remarkable filiform sclereids which resemble slender fibers in their form and unbranched character. These two extremes in sclereid form, however, cannot be sharply demarcated, because of intergradations and because of the strong tendency to fluctuation within many of the entities which have been studied. Under these circumstances, a classification of sclereids based on cell-form must be sufficiently elastic to include not only the outstanding "types" but also the intergradations which exist between them. From this standpoint, a morphological classification of the foliar sclereids of *Mouriria* is now presented. The sequence of arrangement of the four main "types" is mainly one of convenience and is not intended to represent a "phylogenetic series." On the contrary there is no reliable clue at present as to which of these types is "primitive." Therefore such terms as "rudimentary" and "highly developed" are used in a descriptive sense only and carry no evolutionary implications.

TYPE I. The sclereids grouped under this type are characterized by their parenchymatous form and rudimentary branches. Their position is prevailingly terminal at the ends of the veinlets throughout the nineteen species in which they have been encountered. In three species¹, *M. myrtifolia* (all collections except *Ducke 14379*), *M. vernicosa*, and *M. brachyanthera*, occasional sclereids, similar to those at the vein-endings, develop independently within the mesophyll. The sclereids, in the simplest cases observed, are spheroidal cells, unbranched or provided with irregular and short radiating arms. Cells of this kind occur in the leaves of *M. myrtifolia*, *M. Sagotiana*, *M. Valenzuelana*, and *M. vernicosa*. In these species, the secondary wall of the sclereids fluctuates widely in thickness, not only between the different entities but even within the same leaf (figs. 1, 2). A more complex and consistently branched kind of spheroidal sclereid was

¹ If no citations to specimens accompany the name of a species in this article it is to be assumed that *all* of the collections of this entity studied exhibit the same morphological type of sclereid.

found in the leaves of *M. angustifolia*, *M. brachyanthera*, *M. Huberi* (Mexico 5980), *M. nervosa*, *M. Plasschaerti*, *M. Sideroxylon*, and *M. Ulei* (Ducke 205). In these forms, the relatively thick-walled sclereids possess numerous radiating branches which very frequently dichotomize at their tips (fig. 3). Sclereids of a fundamentally similar type were also encountered in the leaves of *M. acuta*, *M. marginata*, *M. parvifolia*, and *M. myrtilloides* (Britton 3998, Harris & Britton 10629). The sclereids in these species tend to develop a more irregular cell-body but they are not sharply distinct from the spheroidal-branched forms described above (fig. 4).

TYPE II. Within this category the writer has attempted to segregate a complex series of ramified sclereids which vary considerably in size, form of the cell-body, and degree of development of the branch-system. Among the extremes in specialization within this polymorphic group are the stellate forms typical for example of the leaves of *M. princeps*, *M. micradenia*, and *M. ciliata* (figs. 6, 7), the dichotomously lobed sclereids with short acute branches which occur in *M. trunciflora* and *M. Hellerei* (figs. 8-10), and the bizarre fusiform irregularly branched cells which are found in the leaves of *M. oligantha*, *M. Chamissoana* var. *paulistana*, and *M. Marshallii* (figs. 13-15). Many fluctuating and intermediate forms occur between these extremes and preclude any efforts at a rigid system of classification. Indeed it seems entirely possible that the examination of a wider range of leaf material than has been possible in this study would reveal even more extensive variations. For purposes of convenience in discussion, however, two rather well-defined trends of specialization are recognized.

(1) *Stellately branched sclereids*. These remarkable cells are characterized by the possession of relatively long and often dichotomizing arms which radiate in various directions from the irregular cell-body (figs. 5-7). In some cases, the tips of the vertical arms may reach the inner walls of one or both epidermal layers, but the major portion of the branch-system is confined within the mesophyll. Sclereids of this kind are prevalently terminal in position, although in *M. rostrata*, *M. monantha*, *M. domingensis*, and *M. grandiflora* occasional examples of isolated sclereids were seen. When the various species exhibiting stellately branched sclereids are compared, interesting and apparently consistent differences in the size, number, and character of the branches are evident. For example, the branch-system of the sclereids of *M. cyphocarpa* (all collections except Williams 9398) consists of a radiating series of dichotomizing arms which seem to represent merely a more vigorous development of the condition described for the sclereids of Type I (cf. figs. 3 and 5). A similar trend in development was also encountered in the sclereids of *M. exilis*. In contrast, the stellate sclereids of *M. princeps*, *M. grandiflora*, *M. ciliata*, *M. collocarpa*, and *M. acutiflora* var. *oligantha* develop long slender arms which extend both laterally and vertically through the mesophyll in a most distinctive manner. Often the arms of adjacent sclereids overlap

to varying degrees (fig. 6). The sclereids of *M. brunneicalyx*, *M. Weddellii*, and *M. micradenia* closely approach this condition but tend to be somewhat shorter and more irregularly branched (fig. 7). In a number of species, the main body of the sclereid, which is somewhat flattened and dichotomously lobed, develops a series of short irregular acute arms which extend toward each epidermal layer. This condition has been observed in *M. trunciflora*, *M. Helleri*, *M. monantha*, *M. buxifolia*, *M. samancensis*, *M. hottensis*, and *M. "aff. spathulata"* (figs. 8-10). Such sclereids, however, in the material examined tend to fluctuate in form and are not sharply demarcated from the more regular stellate types.

The sclereids of *M. brevipes*, although radiately branched, offer several points of morphological interest. In all the collections of this species examined, the sclereid-branches are unusually slender and often appear bent or twisted in a very distinctive manner. In some cases, small terminal portions of certain of the vertical branches extend between the epidermis and the adjacent mesophyll cells.

In concluding this discussion of stellately branched sclereids, it is necessary to correct the apparently erroneous statements of Palézieux (15, p. 76) that "spicular cells" (i.e. sclereids) are absent from the leaf of *M. domingensis*. His conclusions were based upon Puerto Rican material cited as "*Sintensis* 5024." The present investigation, utilizing one collection from Santo Domingo (*Ricksecker* 477) and two collections from Haiti (*Ekman* H4209, *Ekman* H5121), yields quite a different result. In all cases, small radiately branched terminal sclereids were seen, but they are extremely few in number and the majority of the veinlets terminate in normal tracheary elements. A re-examination of Palézieux's material, using large portions of cleared leaves, would therefore seem very desirable.

(2) *Fusiform-branched sclereids*. In a number of species, the sclereids tend to be more or less conspicuously elongated within the mesophyll and the branch-system is correspondingly irregular in character. This trend appears to varying degrees in the sclereids of *M. brachypoda*, *M. Gleasoniana* (*Matuda* 3093), *M. lanceolata* (*Wright* 1235), *M. spathulata* (*Wright* 1234), *M. Lisboa*, *M. sp.* (*Roig* 61 from Cuba), and *M. sp.* (*Acuña* 12602 from Cuba). Excellent examples are provided by the sclereids of *M. Muelleri*, which vary in form from short irregularly branched elements to cells provided with long fiber-like ends (fig. 12). In *M. acutiflora* the sclereids are more profusely branched, with the same tendency, however, to assume an elongated form (fig. 11). But the most striking examples of elongated ramified sclereids were observed in *M. Steyermarkii*, *M. oligantha*, *M. Chamissoana*, *M. Chamissoana* var. *paulistana*, and *M. Marshallii*. In each of these species the sclereids are so distinctive in their morphology that separate description is necessary.

In *M. Steyermarkii* the sclereids are extremely variable in form, ranging from irregularly branched cells with the tips of the branches often reaching the lower epidermis to slender and sparingly branched fiber-like elements. In sclereids of the latter type, the vertical branches are often restricted to

that portion of the element which is in direct contact with the end of the veinlet.

A very distinctive kind of sclereid was discovered in the leaf of *M. oligantha*. The terminal sclereids of this species are exceptionally large in size, very thick-walled, and provided with a series of relatively short, acute spicule-like branches (fig. 13). Although many sclereids are extremely irregular in form, there is a pronounced tendency to the development of a massive fiber-like cell body. When portions of the cleared leaf are observed from both surfaces, it is evident that very short dichotomizing terminations of certain of the branches extend beneath the adaxial epidermis and the mesophyll.

The sclereids of *M. Chamissoana* and *M. Chamissoana* var. *paulistana* are polymorphic to an unusual degree. When even small areas of the cleared leaf are examined it is evident that the range in variation includes (1) short rod-like elements with more or less truncated ends, (2) elongated fusiform cells with few or no branches, and (3) dichotomously branched elements which may appear Y- or X-shaped (fig. 14). In both the fusiform and branched types, the ultimate ends of the cell-body or its arms are blunt rather than acute. A careful study of the position of the sclereids in both of the above entities likewise reveals unusual fluctuation. Many of the veinlets terminate in solitary sclereids of varying form, but diffused sclereids of similar morphology are also frequent. In several instances, pairs of ramified interlocked sclereids were observed lying free in the mesophyll.

The situation in the leaf of *M. Marshallii* is one of the most remarkable encountered in this survey. The submarginal regions of the lamina are largely devoid of sclereids, and only rarely were peculiar thin-walled irregularly branched cells observed at the ends of the veinlets. On the contrary, typical sclereids, in the limited material of this species examined, are restricted to the lamina-margin, where they appear as a series of closely packed massive fiber-like cells (fig. 15). Branching is sparse and irregular and the secondary wall is thick and apparently conspicuously laminated. Careful examination of cleared material reveals that these sclereids are strictly terminal at the ends of the marginal veinlets.

TYPE III. In sclereids of this type, the greatly elongated axis of the cell extends obliquely or vertically through the entire mesophyll and branches more or less profusely beneath each epidermal layer. The characteristic orientation and distinctive branching of sclereids of this type is vividly illustrated in *M. Pusa*. When a thick transection of the cleared lamina of this species is examined, the sclereids appear as columnar elements with numerous overlapping branches extending beneath the lower and upper epidermis (fig. 16). As is evident in this figure, the main axis of these remarkable sclereids frequently dichotomizes, sending out two series of candelabra-like branches toward the upper or lower surface of the lamina. When viewed as isolated cells in macerated material, the sclereids of *M. Pusa* vary widely as to the length of the

terminal branches and their relative development at each end of a given cell. Very commonly the sclereid appears I-shaped because of the prominent development of two horizontal branches at each end of the cell (fig. 37). But many variants of this condition were noted, including T-shaped cells with short root-like branches at one end and forms with one or two candelabra-like branch-systems. The full extent and complexity of the branch-systems of the sclereids of *M. Pusa* is fully appreciated, however, only by the study of large portions of cleared leaves. When the adaxial surface of the lamina is viewed at a high plane of focus, the subepidermal branches of adjacent sclereids are seen to overlap and to interlock in a most intricate manner (fig. 17). In contrast, the branches which develop beneath the abaxial epidermis tend to be somewhat shorter and less crowded in appearance (fig. 18).

Sclereids of a similar morphological type are also found in the leaves of *M. rhizophoraefolia* and *M. Gardneri*. In the former the sclereids tend to be less profusely branched but otherwise are very similar to those of *M. Pusa*. But in *M. Gardneri* the subepidermal branch-systems attain a degree of development which is truly remarkable. As viewed from the adaxial surface, the complex radiating and dichotomizing branches of the sclereids collectively form an intricate mesh-work (fig. 19). This condition is equally apparent when the abaxial surface of the lamina is examined (fig. 20). Here the sclereid-branches are very tightly interlocked and the meshes of the reticulum are occupied by the prominent stomatal crypts which are characteristic of a number of species of *Mouriria* (21, pp. 47-48, pl. 2, figs. 11-15).

Columnar branched sclereids were also encountered in the leaves of *M. cauliflora* and *M. abnormis*. In these species, however, the subepidermal branch-systems are somewhat different in character and are much less extensively developed than in *M. Pusa* and *M. Gardneri*. When cleared leaves of *M. cauliflora*, for example, are examined at a high level of focus, it is evident that a considerable portion of the branch-systems of the rather widely spaced sclereids extends in a dendroid manner below the epidermis (fig. 21). Instructive views of the distinctive sclereids of this species are furnished by macerations. These reveal that the sclereids are columnar in form with remarkable dendroid branch-systems at each end (fig. 35). Often the main axis of the sclereid dichotomizes, thus producing a series of candelabra-like branches (fig. 36). The sclereids of *M. abnormis* are rather similar morphologically, differing mainly in the more conspicuous tendency of the main axis to fork.

With respect to position, the branched sclereids of *M. Pusa*, *M. rhizophoraefolia*, and *M. cauliflora* are strictly terminal at the ends of the veinlets. In *M. abnormis*, however, many of the columnar sclereids develop independently of the vascular system within the mesophyll. Unfortunately no decision could be reached with reference to *M. Gardneri*, because clear views of the veinlets are obscured by the profuse subepidermal branch-systems of the sclereids.

TYPE IV. The sclereids included under this type are distinguished by

their slender greatly elongated form and by their peculiar orientation within the leaf. They were encountered in only nine of the species investigated and are among the most bizarre of the foliar idioblasts found in *Mouriria*.

The striking features of this type of sclereid are well illustrated in *M. anomala*. As seen in transectional view, the lamina of this species appears to be permeated by a tangled series of thread-like cells which traverse the mesophyll in the most varied directions and extend beneath the epidermal layers (fig. 22). The general impression is that of a "diseased leaf" thoroughly penetrated by a fungus mycelium, an impression which is further strengthened when the adaxial surface of cleared leaves is viewed at a high plane of focus (fig. 23). As seen from this aspect the sclereids appear as slender intertwined filiform elements, many of which extend horizontally for a considerable distance beneath the epidermis. An essentially similar appearance is presented when the cleared leaf is examined from the abaxial surface, except that the sclereids "avoid" the stomatal crypts. The latter appear singly or in groups bordered by the interlaced and overlapping ends of the sclereids. A careful inspection of figure 22 will show that a number of the sclereids follow an oblique undulating course through the mesophyll, their opposed ends terminating below the upper and lower epidermis (cf. also 21, pl. 2, fig. 7). Whether this is invariably the orientation of every sclereid is impossible to decide because of the great length and tortuous path of many of the cells. The ultimate solution of this question must come from a study of the complete history of development of the sclereids.

Sclereids entirely similar in form to those of *M. anomala* also occur in the leaves of *M. subumbellata*, *M. crassifolia*, *M. Apiranga*, and *M. eugeniaefolia*. In these species the sclereids are extremely long and are well developed beneath the epidermis, where they are arranged in complex intertwined groups (figs. 24, 28). This arrangement is also shown in a striking fashion at the extreme marginal region of the lamina, where the filiform sclereids are very closely packed and only occasional free tips are evident (fig. 25).

When isolated by maceration, the sclereids of this type appear as long, acuminate fiber-like cells which are bent or twisted to various degrees, as would be expected from their peculiar orientation within the lamina (fig. 39). In all of the species mentioned above, occasional sclereids fork at one or both ends and in addition may be provided with a few short spicule-like branches.

The relation of sclereids of this type to the veinlets could only be satisfactorily determined in *M. Apiranga*. In one of the collections of this species (*da Costa* 124) it was possible to find certain areas in the cleared leaf where the attachment of sclereids to the ends of the veinlets was unmistakable. Whether in this and the other four species the sclereids are *prevalingly* terminal in position can be settled only by ontogenetic study.

For convenience, the writer has also included under Type IV the sclereids of *M. densifoliata*, *M. dumetosa*, *M. arborea*, and *M. Petroniana*.

In these species, the sclereids traverse the mesophyll in various directions but tend to branch, more or less profusely, beneath the epidermal layers. On the basis of morphology and orientation, these sclereids thus appear somewhat intermediate between Types III and IV. When the adaxial surface, for example, of the lamina of *M. densifoliata* is examined, the sclereids appear as acuminate unbranched cells which, except for their shorter extension beneath the epidermis, resemble the sclereids of *M. crassifolia* (cf. figs. 24 and 26). But when the abaxial surface of the leaf of *M. densifoliata* is studied it is clear that the ends of many of the sclereids are forked or irregularly branched, somewhat like the abaxial ends of the sclereids of *M. Pusa* (cf. figs. 18 and 27). This latter resemblance will be clearer by reference to figure 38, which depicts an isolated cell of *M. densifoliata*. This element is decidedly fiber-like at one end, while the opposite end is branched very much like that of the sclereid of *M. Pusa* (cf. figs. 37 and 38). In *M. dumetosa* a study of cleared leaf-sectors indicates that the sclereids are rather coarse fiber-like cells which branch abundantly under both epidermal layers.

The most striking examples of sclereids which seem to combine the morphological characteristics of Types III and IV were found in the leaves of *M. arborea* and *M. Petroniana*. In these species the terminal sclereids are very long slender cells, branched within the mesophyll and with delicate ramifications beneath each epidermal layer (figs. 29, 30). These sclereids appear to be "connecting links" between the extremes in specialization represented on the one hand by the idioblasts of *M. Pusa* and on the other by those of *M. Apiranga* (cf. figs. 17 and 28 with figs. 29 and 30).

DISCUSSION AND SUMMARY

The wide range in sclereid-types which occurs in *Mouriria* and the dominant terminal position of these idioblasts represent problems of considerable morphological and taxonomic interest which will now be examined under two main topics.

(1) TERMINAL POSITION OF THE SCLEREIDS. Throughout the 69 species which have been studied, there is an unmistakable tendency for the sclereids to be restricted in position to the ends of the veinlets, regardless of their form or particular orientation within the leaf (figs. 1-15, 31-34). This distinctive topography, which has apparently not been observed in previous studies on angiosperm sclereids,² raises the question of the onto-

² The relation of the various sclereid-types to the veinlets in *Memecylon* deserves comparative study because of the presumably close systematic relationship of this genus to *Mouriria* (21, pp. 50-51). Although no attempt was made at a comprehensive survey, the writer discovered terminal sclereids in the leaves of the following species: *Memecylon Arnottianum* Wight ex Thwaites (Thwaites 1589, US), *M. obtusum* Wall. (Helfer 126, A), *M. oligoneuron* Bl. (Elmer 21398, Ramex 1635, Yates 1216, UC), *M. phyllanthifolium* Thwaites ex Clarke (Thwaites 3901, isotype US), *M. scutellatum* (Lour.) Naud. (Ching 9757, McClure 20120, UC; Clemens 3313, US), and *M. Spathandra* Bl. (Linder 1305, Dinklage 2971, Kennedy 1844, A; Grossweiler 9189, US).

genetic and phylogenetic origin of the sclereids in *Mouriria*. Are these idioblasts "homologous" with the tracheary or sclerenchymatous elements of the veinlets, or is their terminal position a topographical relationship devoid of morphological significance? Unfortunately, material suitable for ontogenetic study has not been secured by the writer and hence it is not clear whether the terminal sclereids originate from "procambial cells" in the developing veinlets or arise from adjacent cells of the "ground meristem."³ The existence in certain species of both terminal as well as diffuse sclereids has already been mentioned, and developmental studies on the leaves of these plants would doubtless shed important light on the problem. It is of interest, however, that in several of the species investigated indirect evidence is found of the possibly close ontogenetic relationship between terminal sclereids and tracheary elements. The most striking illustration of this was encountered in the leaf of *M. maestralis*. In this Cuban endemic, typical thick-walled ramified sclereids are largely confined to the midrib and marginal regions of the lamina, and the majority of the veinlets terminate in cells intermediate in character between sclereids and tracheary elements. The "hybrid" character of these remarkable cells is shown by their tendency to produce sclereid-like lobes and branches and by the development of helical thickenings closely similar to those of protoxylem elements (figs. 31-33). Not infrequently a group of adjacent veinlets exhibits a series of remarkable intergradations between "normal" tracheary cells and thick-walled branched sclereids (fig. 34). Because the material available for study was restricted in amount, it is uncertain whether the presence of "transitional cells" represents a reliable diagnostic character of *M. maestralis*. The situation in *M. hottensis* clearly demonstrates the need for a cautious approach to such a problem. In one collection of this species (*Ekman 10399*, A) many of the veinlets terminate in hybrid-like cells similar to those in *M. maestralis*. But in a collection of *M. hottensis* bearing the same number, from the U. S. National Herbarium, the majority of the veinlets end in thick-walled irregularly branched sclereids. Such fluctuations make it plain that the question of the ontogenetic and phylogenetic relationships between sclereids and tracheary elements in *Mouriria* requires intensive as well as extensive study.

(2) SYSTEMATIC VALUE OF THE SCLEREIDS. The classification of sclereids proposed in this paper is based entirely on morphological characters and was not influenced by the opinions advanced by various writers as to the systematic affinities between the various species of the genus. This standpoint was obviously demanded, because (1) no comprehensive taxonomic revision of *Mouriria* has been attempted since the publication of Cogniaux's (7) monograph, and (2) a number of the entities used in the

³ Both methods of origin occur in the case of the so-called "storage tracheids" found in the leaves of a number of angiosperms (16, pp. 46-50 and 60-62). In "*Capparis religiosa*" the terminal storage tracheids are branched and resemble, to some extent, certain of the sclereids which occur in *Mouriria* (16, fig. 5).

present survey may subsequently prove to have been incorrectly determined. For these reasons, the possible diagnostic value of the sclereids can be approached only in a most tentative manner.

First of all, it seems evident that the presence of terminal foliar sclereids is an important *generic character* of *Mouriria* which can be utilized especially in the identification of "sterile" or doubtful material. This was illustrated by the study of a series of unclassified specimens, presumably all belonging to *Mouriria*, obtained from the Arnold Arboretum. In one of these specimens (*Ducke* 44) long filiform sclereids, obviously of the type found in *M. crassifolia* and *M. anomala*, are present. In three specimens (*Krukoff* 6565, *Ducke* 173, *Ducke* 299) typical stellately branched terminal sclereids of a type common in *Mouriria* were encountered. But in *Krukoff* 6706 peculiar diffuse sclereids, unrelated to the veinlets, occur. The true affinities of this specimen are obscure, but it does not appear to be a species of *Mouriria*. The generic value of sclereids was also illustrated by the study of a leaf-specimen, presumably of a *Mouriria*, received from the herbarium of the Missouri Botanical Garden under the specific epithet "*Gentlei*" (*Gentle* 1684). When cleared, this leaf proved devoid of sclereids, and a subsequent search in the literature revealed that the same collection was described as *Eugenia Gentlei* (Myrtaceae) by Lundell (13). A further example was provided by the contrast between the two collections of *M. Gleasoniana*. In the leaf of the type collection, from Mexico (*Matuda* 3093), ramified terminal sclereids very similar to those of *M. Muellerei* were found (cf. fig. 12). But in the specimen from Guatemala (*Steyermark* 39525) the leaf is entirely devoid of sclereids and, because of the presence of well developed secretory glands in the mesophyll, appears to represent an entity belonging to the Myrtaceae. In two of the species of *Mouriria* included in the present survey, *M. floribunda* (*Mcxia* 6187), from Peru, and *M. pseudogeminata* (*Williams* 10182), from Venezuela, sclereids are absent from the lamina and the veinlets terminate in lobed or greatly enlarged helically thickened cells. These elements closely resemble the so-called "storage tracheids" of *Nepenthes* (16, fig. 8A). On the basis of the very limited material available, it seems very doubtful to the writer that these specimens were correctly determined.

In any attempt to utilize sclereid-types as an aid in the distinction of species in *Mouriria*, full consideration must be given to the common tendency of sclereids, especially those of Type II, to fluctuate in form within the leaves of the same entity. To determine fully the limits of variation in each case requires the comparison of a much wider range of material than has been possible in the present survey. Nevertheless interesting results emerge when the available morphological data are applied to a discrete and apparently "representative" series of species. The 19 Amazonian species recently discussed from a taxonomic and a phytogeographic standpoint by *Ducke* (8) furnish very suitable material. In the first place there are included among these species a number of the

old and apparently very distinct entities which are treated by Cogniaux (7) in his monograph of *Mouriria*. Secondly, for each of these 19 species, the writer has assembled 2 or more separate leaf-collections, the comparison of which showed excellent general agreement as to sclereid-type. Finally, the specimens of five of the species bear the same number which is cited in Ducke's article. On the basis of sclereid-morphology these Amazonian species can be arranged in four groups as follows:

Group I includes *M. brachyanthera*, *M. Huberi* (Mexia 5980), *M. Plasschaerti*, *M. Ulei* (Ducke 205), *M. nervosa*, *M. Sagotiana*, *M. vernicosa*, and *M. myrtifolia*. In these species the sclereids are parenchymatous in form and are provided with rudimentary branches (figs. 1-3). No significant variations in sclereid-type were encountered except in *M. Ulei* (HJBR from Pará), *M. myrtifolia* (Ducke 14379), and *M. Huberi* (HJBR from Pará), in which the sclereids are more irregularly and profusely branched, resembling those of *M. elliptica* and *M. acutiflora* (fig. 11). On this point it is interesting to note that Ducke (8) states that *M. Huberi* is the only species of Amazonia belonging to the subgenus *Olisbea*. The latter was originally defined as one of the two "sections" of *Mouriria* by Cogniaux (7), to include *M. elliptica*, *M. rhizophoraefolia*, *M. arborea*, and *M. Petroniana*.

Group II includes *M. trunciflora*, *M. collocarpa*, *M. micradenia*, *M. grandiflora*, and *M. acutiflora*. The sclereids of all these species are profusely ramified but appear to differ from one another in the form of the cell and the extent of the branch-system (figs. 7-11). Because of this, the sclereids may ultimately prove useful in the differentiation of these five species. The presence of numerous small diffuse sclereids appears to be an additional diagnostic feature of *M. trunciflora* (fig. 10).

Group III includes *M. cauliflora*, which appears very distinctive because of (1) the columnar terminal sclereids with their subepidermal branch-systems, and (2) the presence of parenchymatous diffuse sclereids (figs. 21, 35, 36). *Mouriria guianensis* may also belong in this group, although this species has proved the most variable of all the entities investigated with respect to sclereid-morphology. In some collections (Drouet 2356) the terminal sclereids are irregular columnar cells which branch irregularly beneath the upper epidermis of the leaf. In other collections (Williams 11600, Krukoff 6613) the sclereids closely approach the type found in *M. acutiflora*. Because of such fluctuations it seems possible that the writer's leaf-collections of *M. guianensis* may represent several distinct entities.

Group IV includes *M. anomala*, *M. crassifolia*, *M. Apiranga*, and *M. dumetosa*. In these species the sclereids are greatly elongated fiber-like cells branched to varying degrees beneath the epidermis and oriented in a most distinctive manner in the leaf (figs. 22-24, 28, 39).

Whether these "species groups" just defined on the basis of sclereid-morphology are composed of entities which are closely related in other respects is open to question. In this connection it is worthy of note that

Cogniaux's (7) division of *Mouriria* into two sections results in the *separation* of species which exhibit similar morphological types of sclereids. Thus, for example, *M. Gardneri* and *M. Pusa* are classed by Cogniaux under the section *Eumouriria*, while *M. rhizophoraeifolia* is placed in the section *Olisbea*. All three species, however, form distinctive columnar sclereids which branch more or less profusely beneath the epidermal layers (figs. 16-20). Similarly *M. arborea* and *M. Petroniana* are segregated from *M. crassifolia*, *M. dumetosa*, *M. eugeniaefolia*, *M. subumbellata*, and *M. Apiranga*, although all of these species possess slender fiber-like sclereids which are among the most distinctive idioblasts in the genus (figs. 22-25, 28-30). Such apparent discrepancies, however, do not necessarily indicate that sclereid-characters are less reliable than other morphological criteria⁴ in judging affinities between species. On the contrary, it is clear that the ideal approach to the systematics of *Mouriria* should involve the comparison and correlation of a wide range of morphological features, including floral structure as well as the histology of the leaf and stem. The important results which emerge from a broad attack of this sort are illustrated by the recent collaborative studies of Smith (17, 18, 19), Bailey and Nast (1, 2, 3, 4, 5, 6), and Nast (14) on the Winteraceae.

⁴ Cogniaux (7) used certain characters of the calyx and pollen as the bases for his two sections of *Mouriria*.

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EXPLANATION OF PLATES

PLATE I

Cleared leaves showing terminal sclereids of Type I. Magnification $\times 140$. FIG. 1. *M. myrtifolia* Spruce, *Krukoff* 1371. FIG. 2. *M. Sagotiana* Triana, *Klug* 1501. FIG. 3. *M. brachyanthera* Ducke, *Mexia* 5964. FIG. 4. *M. emarginata* Griseb., *Ekman* 9280.

PLATE II

Cleared leaves showing terminal sclereids of Type II. Magnification $\times 140$. FIG. 5. *M. cyphocarpa* Standley, *Schipp* 70. FIG. 6. *M. princeps* Naud., *Krukoff* 5459. FIG. 7. *M. micradenia* Ducke, *Ducke* 25520. FIG. 8. *M. Helleri* Britton, *Heller* 1372.

PLATE III

Cleared leaves showing terminal sclereids of Type II. Magnification $\times 140$. FIG. 9. *M. trunciflora* Ducke, *Ducke* 16937. FIG. 10. A different region of the same leaf shown in fig. 9. Note small diffuse sclereids in mesophyll and along the two veins. FIG. 11. *M. acutiflora* Naud., *Ule* 7677. FIG. 12. *M. Muellerei* Cogn., *Matuda* 3093.

PLATE IV

Cleared leaves showing terminal sclereids of Type II. Magnification $\times 140$. FIG. 13. *M. oligantha* Pilger, *Williams* 3904. The globoid structures in the center and right-hand portions of the figure are masses of crystals. FIG. 14. *M. Chamissoana* var. *paulistana* Hoehne, *Hoehne* 29921. FIG. 15. *M. Marshallii* Burt & Sandwith, *Russell* 1265-9. Margin of lamina showing large fusiform-branched sclereids. The dark bodies near the sclereids are masses of crystals.

PLATE V

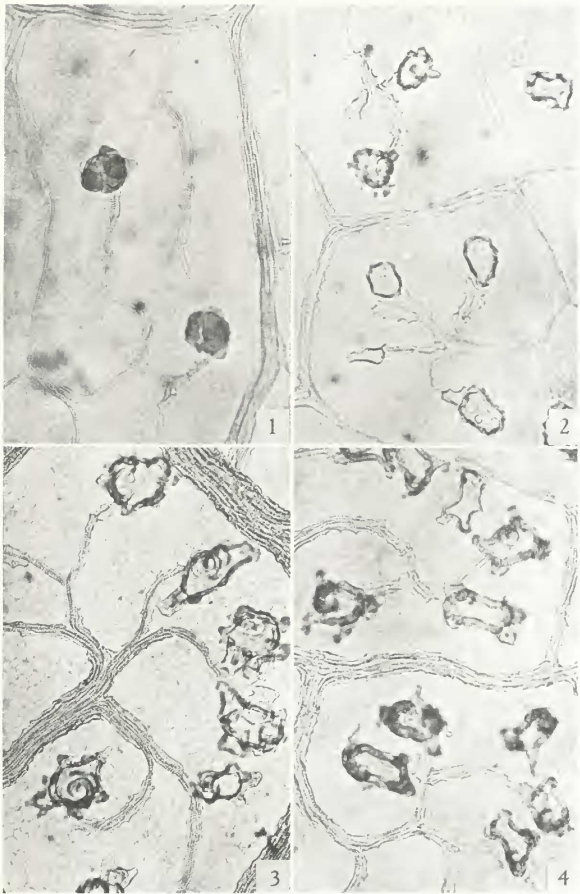
Cleared leaves of *M. Pusa* Gardn., *Gardner* 2596, illustrating form and orientation of Type III sclereids. Magnification $\times 140$. FIG. 16. Thick transection of lamina showing columnar sclereids branched beneath the epidermal layers. Note veinlet in center of figure. FIG. 17. Adaxial surface of lamina showing sclereid-branches under the epidermis. FIG. 18. Abaxial surface of lamina showing sclereid-branches under the epidermis.

PLATE VI

Cleared leaves illustrating sclereids of Type III. Magnification $\times 140$. FIG. 19. *M. Gardneri* Triana, *Gardner* 2863. Adaxial surface of lamina showing the profusely developed subepidermal branch-systems of the sclereids. FIG. 20. Abaxial surface of a portion of the same leaf shown in fig. 19. The stomatal crypts, appearing as oval areas, are bordered by the tightly interlocked subepidermal branches of the sclereids. FIG. 21. *M. cauliflora* DC., *Ducke* 25517. Abaxial surface of lamina showing dendroid branching of the terminal sclereids beneath the epidermis. Note the small parenchymatous diffuse sclereids lying in the mesophyll.

PLATE VII

Cleared leaves illustrating sclereids of Type IV. Magnification $\times 140$. FIG. 22. *M. anomala* Pulle, *Ducke* 14373. Thick transection of lamina showing the very numerous intertwined filiform sclereids which traverse the mesophyll region and extend beneath the epidermal layers. FIG. 23. Adaxial surface of a portion of the



FOLIAR SCLEREIDS IN MOURIRIA